PALAEOSMUNDA, A NEW GENUS OF SIPHONOSTELIC OSMUNDACEOUS TRUNKS FROM THE UPPER PERMIAN OF QUEENSLAND

by R. E. GOULD

ABSTRACT. Petrified osmundaceous trunks from the Upper Permian coal measures of the Bowen Basin, Queensland, are assigned to a new genus, *Palaeosmunda*, which possesses an ectophloic, sometimes almost simple but usually dictyoxylic, siphonostele with parenchymatous pith; the stems bear stipulate petiole bases which contain sclerotic rings that are rhomboidal in transverse section, upwards becoming laterally extended into flanges. These are the first Permian Osmundaceae definitely known to exhibit a distinct pith and leaf gaps. A table of morphological comparisons of all known Permian osmundaceous axes is presented. Discovery of *Palaeosmunda* indicates that the family had a greater structural diversity and a wider geographic distribution in the Upper Permian than was previously realized; and hence the Osmundaceae probably developed before the Permian. Two species, *P. williamsii* (type species) and *P. playfordii*, are described in detail; the inner cortex, and sometimes the stipules of the petiole bases of *P. williamsii* contain strands of sclerenchyma, while stipules and inner cortex of the petiole bases of *P. playfordii* consist only of parenchyma. Evidence from association indicates that the trunks probably bore fronds of the types referred to *Sphenopteris lobifolia* Morris 1845, *S. polymorpha* Feistmantel 1876, and *Cladophlebis roylei* Arber 1901.

TRUNKS and rhizomes characteristic of the Osmundaceae are apparently well suited to preservation as fossils and the geological history of the family, based on petrified stems, extends from Upper Permian to Recent (Andrews 1961, Miller 1967). Prior to the present work, all known specimens of Permian osmundaceous stems came from the Soviet Union; where the stele is preserved, these contain a protostele or at least an ectophloic siphonostele without well-developed leaf gaps.

Osmundaceous trunks, petrified with silica, calcite, and ferruginous material, occur at many localities in the Upper Permian coal measures of the Bowen Basin, Queensland (text-fig. 1). These are described as two species of a new genus, *Palaeosmunda* gen. nov., in which the stele is usually an ectophloic dictyoxylic siphonostele, but can appear almost simply siphonostelic; the petiole bases are very similar to those of other stipulate Permian osmundaceous stem genera. The new genus is unusual in that it is the first Permian member of the family definitely known to exhibit a distinct pith and leaf gaps.

The specimens on which the study is based were collected by Dr. J. Armstrong, Mr. R. Lees, Dr. B. Runnegar, Dr. F. W. Whitehouse, Mr. J. H. Williams, and the author. Mr. W. A. Hansen and the management and staff of Utah Development Company provided considerable assistance in the location and collection of specimens from Utah's Blackwater coal-mining lease. One specimen, collected in June 1956, was already held in the collections of the Department of Geology and Mineralogy, University of Queensland. All specimens are housed in the Department and catalogue numbers are prefixed UQ.

In his study of the morphology of the living Osmundaceae, Hewitson (1962, p. 80) used the term 'bundle' when describing the stem xylem in transverse section; he considered two (or more) xylem strands connected by even one tracheid as a single bundle. This terminology avoids any confusion when counting the xylem strands, and is very

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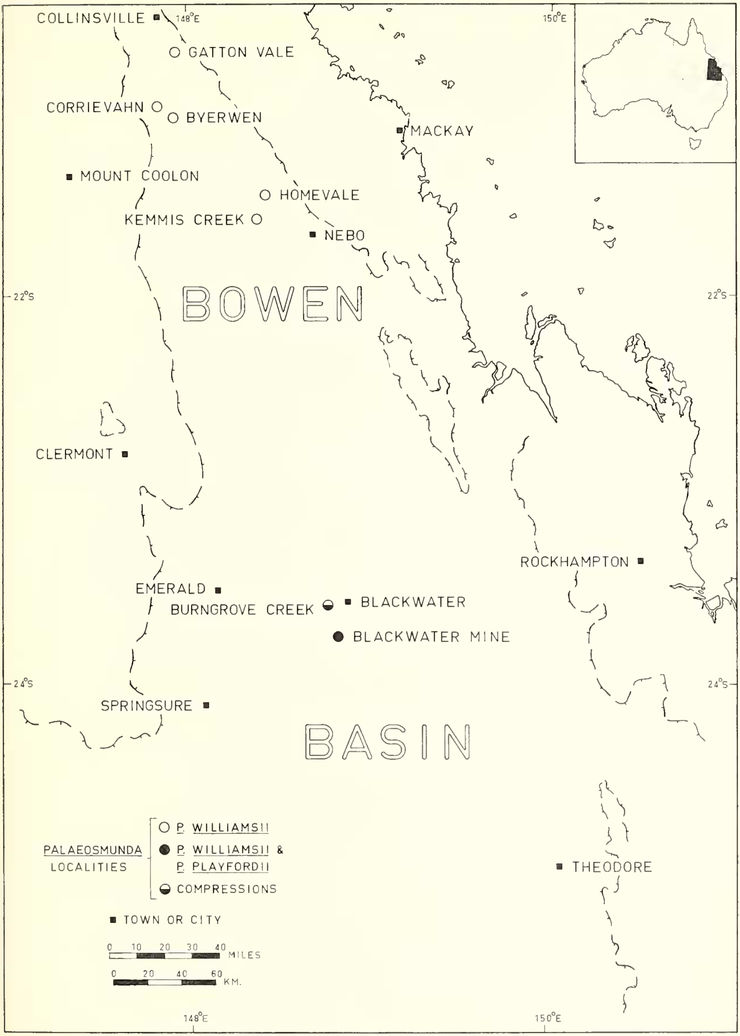


TEXT-FIG. 1. Locality map.

useful in describing the stems of the family where the dictyoxylic stele is well developed. However, where the number of gaps in the xylem ring is small, the number of 'bundles' does not give a complete indication of the structure of the ring. Instead, in the following descriptions, the number of gaps appearing in a transverse section of the xylem cylinder is given. This is equal to the number of bundles in the sense of Hewitson, provided that there are two or more gaps; no gap, or one, results in one 'bundle'. The term 'radial strand' is used in this paper to designate any group of stelar xylem tracheids with a prominent radial dimension when seen in transverse section, regardless of whether the group is connected to adjacent strands or not.

Previous literature. In the second and third parts of their classic memoir on the fossil Osmundaceae, Kidston and Gwynne-Vaughan (1908, 1909) published the first detailed anatomical accounts of Upper Permian osmundaceous stems. They described five species from the Upper Permian of the U.S.S.R., *Zalesskya gracilis* (Eichwald) Kidston and Gwynne-Vaughan 1908, *Z. diploxylon* Kidston and Gwynne-Vaughan 1908, *Thamnopteris schlechtendalii* (Eichwald) Brongniart 1849, *Bathypteris rhomboidea* (Kutorga) Eichwald 1860, and *Anomorrhoea fischeri* Eichwald 1860. The steles of *B. rhomboidea* and *A. fischeri* were not present in their specimens and that of *B. rhomboidea* was described later by Zalessky (1924). Seward (1910) figured some of Kidston and Gwynne-Vaughan's slides and one of these, his frontispiece of *T. schlechtendalii*, had not been figured previously.

In a series of papers, Zalessky (1924, 1927, 1931*a*, *b*, 1935) described and figured further examples from the Upper Permian of the U.S.S.R.; these comprise *B. rhomboidea*, *T. kidstoni* Zalessky 1924, *T. gwynne-vaughani* Zalessky 1924, *Z. uralica* Zalessky 1924, *A. fischeri*, *T. schlechtendalii*, *Z. gracilis*, *Z. diploxylon*, *T. kazanensis* Zalessky 1927, *Z. fistulosa* (Eichwald) Zalessky 1927, *Petcheropteris splendida* Zalessky 1931*a*, *Chasmatopteris principalis* Zalessky 1931*b*, and *Iegosigopteris javorskii* Zalessky 1935. *Thamnopteris kazanensis* was not formally described but a transverse section and some details were figured with explanation (Zalessky 1927, pp. 26, 44, pl. 24, figs. 1–4); the specimen is poorly preserved. Knowledge of *Z. fistulosa* is limited to a photograph of its external surface (Zalessky 1927, pp. 31, 48, pl. 32, fig. 3).

Posthumus (1931) compiled synonymy lists for the genera and species of Permian and other osmundaceous stems that had been described prior to 1928.

STRATIGRAPHY

All specimens of *Palaeosmunda* were collected from the Bowen Basin in freshwater sediments which have been referred to as the Upper Bowen Coal Measures (Smith 1958, Hill and Denmead 1960). Devine and Power (1967) have assigned these sediments in the central western Bowen Basin, including the Blackwater district, to the Bandanna Formation (Power 1967 usage, formerly Upper Bandanna Formation of Patterson *in* Webb 1956, p. 2330). The localities for the osmundaceous fossils (text-fig. 1) are all within the Blackwater Group (Malone 1966) as shown on the geological map of the basin compiled by Malone, Olgers, Mollan, and Jensen (1967); in the Blackwater district the fossil trunks occur in the upper two units of the group, the Burngrove Formation and the Rangal Coal Measures. The Blackwater Group and Bandanna Formation are the same lithological unit in the Blackwater–Springsure area (Power 1967, Devine and Power 1967). The age of the Upper Bowen Coal Measures, Bandanna Formation, and Blackwater Group is generally considered to be Upper Permian (e.g. Runnegar 1968). Webb and McDougall (1967, pp. 483–4) reported an isotopic age of 240 m.y. for a basal part of the Blackwater Group. Ammonoids from horizons below the coal measures in the northern part of the basin are considered to be of Artinskian (Aktastinian–Baigendzhinian) age (Armstrong, Dear, and Runnegar 1967), while microfloras from the Rewan Formation, which overlies the coal measures, are probably in part of Scythian (Otoceratan) age (Evans 1966, p. 59).

SYSTEMATIC PALAEOBOTANY

Division PTEROPHYTA
Order FILICALES
Family OSMUNDACEAE
Genus PALAEOSMUNDA gen. nov.

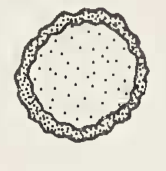
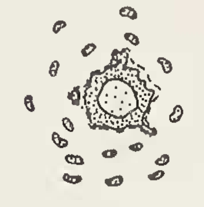
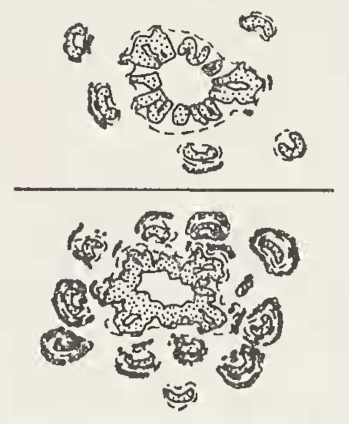
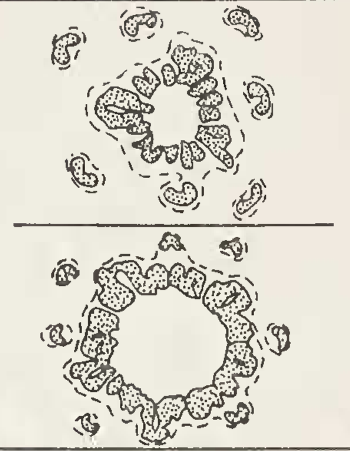
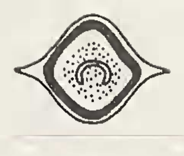
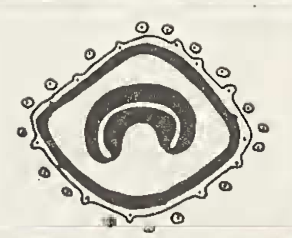
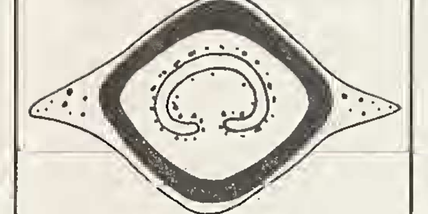
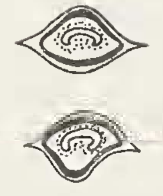
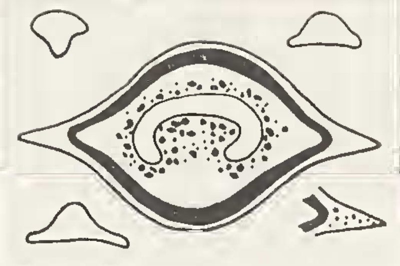
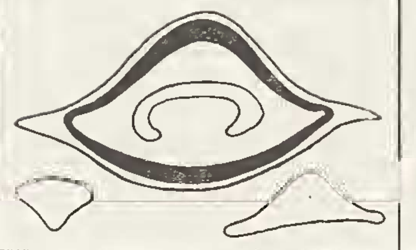
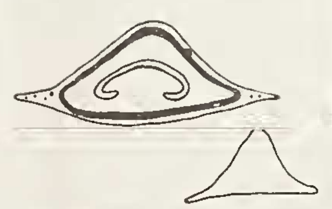
Type species. Palaeosmunda williamsii sp. nov.

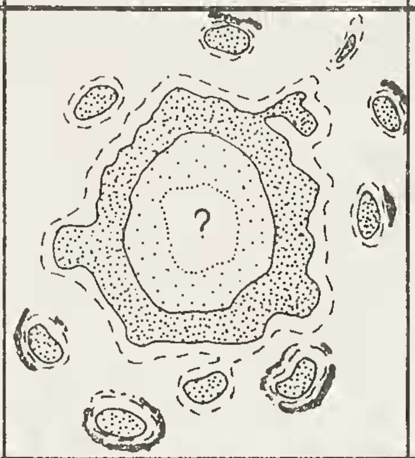
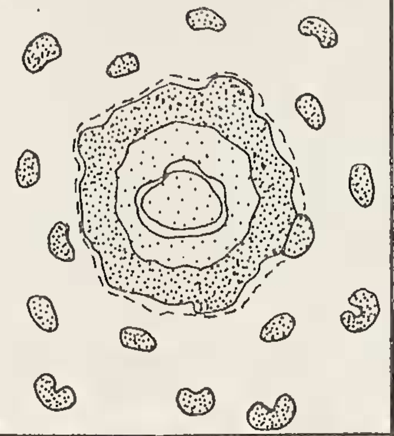
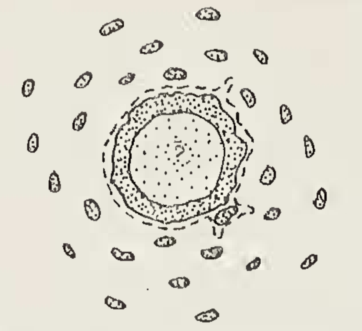
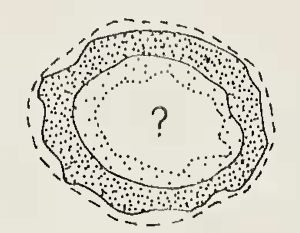
Diagnosis. Arborescent osmundaceous trunks, each with a stem surrounded by a mantle of leaf bases and adventitious roots; branching of stem dichotomous. Stele an ectophloic, generally dictyoxylic, siphonostele, sometimes almost simply siphonostelic; pith parenchymatous; xylem ring with 0–13 gaps, consisting of 14–28 more or less contiguous radial strands, 9–19 tracheids thick; development of leaf gaps immediate, delayed, or incomplete; gaps very short to long; phloem, pericycle, and endodermis external only. Cortex differentiated into inner parenchymatous zone and outer sclerotic fibrous layer, the latter with short, wide, sclerenchyma cells lining leaf traces and inner cortex; inner cortex about as wide as outer cortex; leaf traces arise at 10–35° to stele, initially with 1 or 2 endarch protoxylem groups; 12–43 traces in a transverse section of cortex. Petiole bases stipulate, containing an adaxially curved, C-shaped vascular strand, inner cortex, and sclerotic ring; sclerotic rings somewhat rhomboidal in cross-section, upwards becoming laterally extended into flanges which partially or completely replace the stipules; rings with gradual increase of fibre diameter towards inner cortex of petiole base, otherwise homogeneous; lateral extremities of ring usually thinner than abaxial and adaxial portions. Roots with diarch xylem strand, arising in pairs from each departing leaf trace usually before it enters inner cortex, or rarely singly, directly from stele; roots often branched and forming dense mat outside mantle.

Discussion. Palaeosmunda differs from the Permian osmundaceous stem genera *Bathypteris* Eichwald 1860, *Chasmatopteris* Zalessky 1931*b*, *Iegosigopteris* Zalessky 1935, *Petcheropteris* Zalessky 1931*a*, *Thamnopteris* Brongniart 1849, and *Zalesskya* Kidston and Gwynne-Vaughan 1908, in that the stele is an ectophloic, usually dictyoxylic, siphonostele with homogeneous metaxylem and a parenchymatous pith; the leaf traces in *Palaeosmunda* initially have one or two endarch protoxylem groups whereas the leaf traces of these other genera are initially mesarch. *Palaeosmunda* lacks both the wide cortex of *Zalesskya* and the spinose petiole bases of *Bathypteris*. There is insufficient information available on *Anomorrhoea* Eichwald 1860, for any useful generic distinction to be made. A table of comparisons of the species of Upper Permian osmundaceous stems is given in folder.

Osmundacaulis Miller 1967 (an organ genus based on '*Osmundites*' *skidegatensis* Penhallow 1902), which occurs in Mesozoic and Tertiary strata, would include stems similar to those of the new genus, but the petiole bases of *Palaeosmunda* are quite different. Besides being of specific importance, the arrangement of sclerenchyma within the petiole base in the Osmundaceae, as well as the anatomy of the stele, is of generic and subgeneric significance (Kidston and Gwynne-Vaughan 1907, Hewitson 1962, Miller 1967). The leaf bases of *Palaeosmunda* can be more closely compared with those of *Anomorrhoea*, *Chasmatopteris*, *Iegosigopteris*, *Petcheropteris*, and *Thamnopteris* than with those of *Osmundacaulis*. The generally rhomboidal to laterally extended shape of the sclerotic ring in transverse section is exhibited by all the Permian genera except *Zalesskya*, in which the leaf bases are unknown. In contrast, the sclerotic rings of *Osmundacaulis* are generally rounded; the leaf traces in the outer cortex of the Jurassic *O. gibbiana* (Kidston and Gwynne-Vaughan) Miller 1967, are, however, rhomboidal in transverse section (Kidston and Gwynne-Vaughan 1907). The initial rhomboidal shape, small stipules, and upward lateral extension of the sclerotic ring into flanges which replace the stipules are well developed in *Palaeosmunda*; the shape is not solely due to the close arrangement of the bases around the stem, as they retain and even increase the laterally flanged shape in the outer part of the mantle where they are free of any restriction. The gradual increase in diameter of the fibres of the sclerotic ring towards the inner cortex of the petiole base is also exhibited by *T. schlechtendalii*, *B. rhomboidea*, and possibly by *A. fischeri* and *I. javorskii* (see Kidston and Gwynne-Vaughan 1909, pl. 5, fig. 36; pl. 7, fig. 48; pl. 8, fig. 63; Zalessky 1935, pl. 2, fig. 7), as well as some post-Palaeozoic species of Osmundaceae. At least *I. javorskii* and *P. splendida*, and possibly also *A. fischeri*, *C. principalis*, and *T. schlechtendalii* (see Zalessky 1927, pl. 23, fig. 1), show relatively thin lateral extremities of the sclerotic ring as in *Palaeosmunda*.

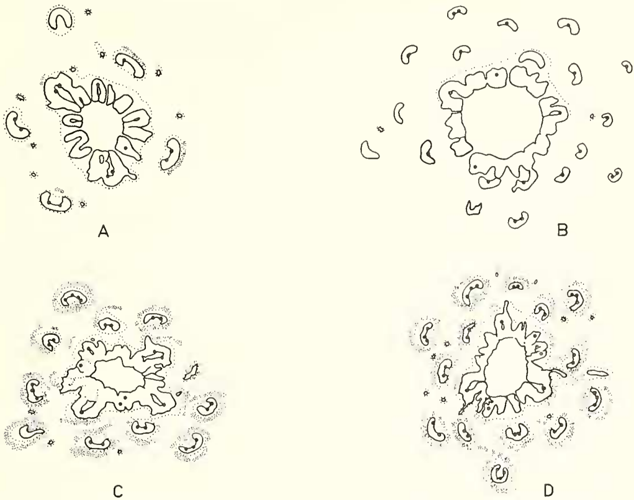
The development of the ectophloic dictyoxylic siphonostele in Osmundaceae by Upper Permian is somewhat earlier than had been previously thought (e.g. Hewitson 1962, p. 84), but is not altogether surprising. Leaf gaps are partially formed in the Upper Permian *C. principalis*, and *T. kidstoni*, also of Upper Permian age, contains some parenchyma cells in the inner xylem. Triassic representatives of osmundaceous stems include *Osmundacaulis herbstii* (Archangelsky and de la Sota) Miller 1967, '*Osmundites*' *tuhajkuensis* Prynada (Orlov 1963, pl. 29, fig. 10), and probably '*Osmundites*' *winterpockensis* Bock 1960; all of these are of Upper Triassic age and *O. herbstii*, and probably '*O.*' *tuhajkuensis*, exhibit dictyoxylic siphonosteles. The shape of the transverse section of the sclerotic ring in the leaf bases of '*O.*' *tuhajkuensis* is somewhat intermediate between those of the Permian examples and *Osmundacaulis*; the two masses of sclerenchyma in each arm of the C-shaped petiolar strand of '*O.*' *tuhajkuensis* has, however, only been found in *Osmundacaulis* and *Osmunda*. '*Osmundites*' *winterpockensis* is based on a sandstone cast with no internal structure preserved (C. N. Miller, pers. comm. 1969). Other Triassic fossil stems referred to the Osmundaceae, and used as examples to explain the evolution of the dictyoxylic siphonostele from the protostele (e.g. Daugherty 1960, Emberger 1962, Arnold 1964, Surange 1966), actually belong to other groups. These include *Chinlea campii* Daugherty 1941, and *Osmundites walkeri* Daugherty 1941, which are synonymous and belong to the Lepidophyta (Miller 1968), and the ectophloic

	ANOMORRHOEA FISCHERI	BATHYPTERIS RHOMBOIDEA	CHASMATOPTERIS PRINCIPALIS	IEGOSIGOPTERIS JAVORSKII	PALAEOSMUNDA WILLIAMSII	PALAEOSMUNDA PLAYFORDII	PETCHEROPTERIS SPLENDIDA
TRANSVERSE SECTION OF STELE	?	 RECONSTRUCTION					
NUMBER & POSITION OF PROTOXYLEM GROUPS IN LEAF TRACE AS IT LEAVES STELE	?	1 ENDARCH IN INNER CORTEX	1 ADAXIALLY MESARCH	1 MESARCH	1-2 ENDARCH	1 ENDARCH	1 MESARCH
NUMBER & POSITION OF PROTOXYLEM GROUPS IN LEAF TRACE AS IT ENTERS OUTER CORTEX OF STEM	1 ENDARCH	?	4 ENDARCH	2 ENDARCH	(1)2-4 ENDARCH	(1)2 ENDARCH	SEVERAL (›1-2) ENDARCH
NUMBER OF PROTOXYLEM GROUPS IN LEAF TRACE AS IT ENTERS BASE OF PETIOLE	?(›2)	?	10-12+	6-10+	4-12	4-10	? MANY
ROOTS:— XYLEM TRACE: ORIGIN:	DIARCH ?	DIARCH & TRIARCH PROBABLY FROM STELE	DIARCH FROM STELE	DIARCH RARELY TRIARCH FROM STELE OR DEPARTING LEAF TRACES	DIARCH MAINLY FROM DEPARTING LEAF TRACES ALSO FROM STELE	DIARCH RARELY TRIARCH MAINLY FROM DEPARTING LEAF TRACES ALSO FROM STELE	DIARCH FROM STELE
NUMBER OF LEAF TRACES IN A TRANSVERSE SECTION OF INNER CORTEX OF STEM	?	?	?14-16	20-26	5-25	6-21	?
NUMBER OF LEAF TRACES IN A TRANSVERSE SECTION OF OUTER CORTEX OF STEM	?20-24	?	?10-12	29-34	7-26	9-19	?
TRANSVERSE SECTION OF PETIOLE BASE							
PETIOLE BASES IN MANTLE:	CLOSELY APPRESSED	LOOSELY APPRESSED, BUT NOT OPEN	CLOSELY APPRESSED	CLOSELY APPRESSED	CLOSELY APPRESSED NEAR STEM; CAN BE OPEN FURTHER OUT	CLOSELY APPRESSED NEAR STEM, USUALLY OPEN FURTHER OUT	CLOSELY APPRESSED NEAR STEM, OPEN FURTHER OUT
REMARKS	POSSIBLY REFERABLE TO THAMNOPTERIS		PROBABLY REFERABLE TO THAMNOPTERIS	PROBABLY REFERABLE TO THAMNOPTERIS			PROBABLY REFERABLE TO THAMNOPTERIS
SOURCES OF DATA	KIDSTON & GWYNNE-VAUGHAN 1909 ZALESSKY 1927	KIDSTON & GWYNNE-VAUGHAN 1909 ZALESSKY 1924, 1927	ZALESSKY 1931b	ZALESSKY 1935	THIS PAPER	THIS PAPER	ZALESSKY 1931a

	THAMNOPTERIS SCHLECHTENDALII	THAMNOPTERIS GWYNNE-VAUGHANI	THAMNOPTERIS KAZANENSIS	THAMNOPTERIS KIDSTONI	ZALESSKYA GRACILIS	ZALESSKYA DIPLOXYLON	ZALESSKYA URALICA
TRANSVERSE SECTION OF STELE						 PART RECONSTRUCTION	
NUMBER & POSITION OF PROTOXYLEM GROUPS IN LEAF TRACE AS IT LEAVES STELE	1(2) MESARCH	1 MESARCH	?1 MESARCH	1 MESARCH	1 MESARCH	PROBABLY 1 MESARCH	1 MESARCH
NUMBER & POSITION OF PROTOXYLEM GROUPS IN LEAF TRACE AS IT ENTERS OUTER CORTEX OF STEM	4-5 ENDARCH	2-3 ENDARCH	AT LEAST 2 ENDARCH	4-5 ENDARCH	2-3 ENDARCH	SEVERAL ENDARCH	2-3 ENDARCH
NUMBER OF PROTOXYLEM GROUPS IN LEAF TRACE AS IT ENTERS BASE OF PETIOLE	10-12+	?5-9	?	?	?	?	?(›4)
ROOTS:— XYLEM TRACE: ORIGIN:	DIARCH FROM STELE OR LEAF TRACES	DIARCH FROM LEAF TRACES	DIARCH ?	DIARCH FROM LEAF TRACES	DIARCH FROM STELE BELOW DEPARTING LEAF TRACES	DIARCH FROM STELE BELOW DEPARTING LEAF TRACES	DIARCH FROM STELE
NUMBER OF LEAF TRACES IN A TRANSVERSE SECTION OF INNER CORTEX OF STEM	20-24	40-44	MANY	23-25	140-160	60-65+	100+
NUMBER OF LEAF TRACES IN A TRANSVERSE SECTION OF OUTER CORTEX OF STEM	16-20	?20-30	?	?5-6	?(7-8+)	?	?(12-16+)
TRANSVERSE SECTION OF PETIOLE BASE		? NO SCLERENCHYMA IN STIPULES			?	?	?
PETIOLE BASES IN MANTLE:	CLOSELY APPRESSED	CLOSELY APPRESSED NEAR STEM, OPEN FURTHER OUT	CLOSELY APPRESSED	? CLOSELY APPRESSED NEAR STEM	?	?	?
REMARKS					CORTEX	COMPARATIVELY	CLOSELY COMPARABLE TO Z. GRACILIS WIDE
SOURCES OF DATA	KIDSTON & GWYNNE-VAUGHAN 1909 SEWARD 1910 ZALESSKY 1927	ZALESSKY 1924, 1927	ZALESSKY 1927	ZALESSKY 1924, 1927	KIDSTON & GWYNNE-VAUGHAN 1908 ŽALESSKY 1924, 1927	KIDSTON & GWYNNE-VAUGHAN 1908 ZALESSKY 1927	ZALESSKY 1924, 1927

TEXT-FIG. 2. Morphological comparisons of Upper Permian osmundaceous stems; *Zalesskya fistulosa* (Eichwald) Zalessky, 1927, is omitted as no details are known. Transverse sections of stele *c.* ×2; inner xylem open stipple, cells not preserved in central portions containing question marks; outer xylem close stipple; details of *Thamnopteris kazanensis* Zalessky, 1927, unknown. Transverse sections of leaf bases *ca.* × 1·55; sclerenchyma black; stippled area in inner cortex of *Anomorrhoea fischeri* Eichwald, 1860, may be sclerenchymatous; outlines show alternate shapes of sclerotic rings.

siphonostelic *Itopsidema vancleavii* Daugherty 1960, which is also probably not a member of the Osmundaceae (Miller 1969). On the other hand, the plants with protosteles and those with ectophloic dictyoxylic siphonosteles may have already been separate groups by the Upper Permian.



TEXT-FIG. 3. *Palaeosmunda williamsii* gen. et sp. nov. Transverse sections of stele and inner cortex, *c.* ×3·5; where discernible, protoxylem groups of xylem ring and leaf traces represented as black dots; endodermis by a dotted line; and generalized position of sclerenchyma strands in inner cortex by close stipple. A, UQF53542; B, UQF50620; C, D, UQF21571 (holotype).

The oldest known petrified axes referable to the Osmundaceae all occur in Upper Permian strata and these are compared in text-fig. 2. In view of the structural diversity and wide geographic distribution exhibited by these axes, and the relatively stable development of the family from Mesozoic to Recent, it is reasonable to assume that the Osmundaceae originated well before the Upper Permian, probably even before the Permian.

Absence of cataphylls in all specimens of *Palaeosmunda* from the Bowen Basin probably indicates that the climate in which the plant grew lacked severe winters (Steeves and Wetmore 1953; Miller 1967, p. 144). It is interesting to note that cataphylls have not been found in any of the Permian osmundaceous axes.

Palaeosmunda williamsii sp. nov.

Plate 1, figs. 1, 2; Plate 2, figs. 1–7; Plate 3, figs. 1–8; Plate 4, figs. 1–10; text-figs. 2, 3

Holotype. UQF21571; figured in Plate 1, figs. 1, 2; Plate 2, figs. 1, 2, 6, 7.

Type locality. Beside the Collinsville–Mt. Coolon Road in Portion 4, Parish of Corrievahn, central Queensland (shown on text-fig. 1 as Corrievahn); Blackwater Group (formerly Upper Bowen Coal Measures).

Derivation of name. The species is named in honour of Mr. J. H. Williams (Mackay) who kindly assisted in the collection of specimens from the northern part of the Bowen Basin.

Diagnosis. Palaeosmunda trunks up to 22 cm. in diameter; stems 1–3·6 cm. wide. Stele an ectophloic dictyoxylic siphonostele, sometimes appearing simply siphonostelic, 3·5–8 mm. in diameter; pith diameter 1–4 mm.; xylem ring 0·7–2·2 mm. wide, with 0–9 gaps, composed of 15–28 radial strands, 9–17 tracheids thick; metaxylem tracheids 35–260 μ (usually 50–150 μ) in diameter, with regular scalariform pitting in 1–5 vertical series on each wall. Inner cortex parenchymatous, sometimes with fibrous sclerenchyma strands surrounding leaf traces; inner cortex 0·8–5·5 mm. wide, including 5–25 leaf traces in a given transverse section; fibrous outer cortex 2·5–9 mm. wide, with 7–26 leaf traces in a transverse section. Leaf traces arise with 1 or 2 endarch protoxylem groups which usually bifurcate before they enter outer cortex; strands of sclerenchyma surround leaf trace in outer cortex of stem, and vascular trace in inner cortex of petiole base. Stipules parenchymatous, or with up to 30, generally small, scattered strands of sclerenchyma fibres.

Description

General. There are 16 specimens, each consisting of a stem surrounded by a mantle of adhering leaf bases and adventitious roots (e.g. Pl. 1, fig. 1; Pl. 3, figs. 1, 7). The specimens are up to 21 cm. long and 22 cm. in diameter, and both ends are broken across. Some trunks are circular in cross-section, but others are oval, presumably due to compression. Three specimens show dichotomy of the stem, but only one contains the actual branching region. The stems, bounded by the sclerotic outer cortex, are 1–3·6 cm. in diameter; the outline in transverse section is undulose due to the emerging petioles.

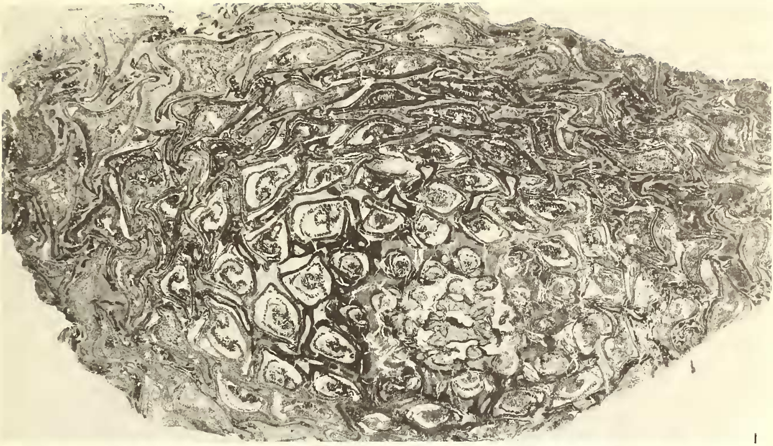
Stele. The pith is 1–4 mm. in diameter (Pl. 2, figs. 4–7; Pl. 3, figs. 4–6), and consists of vertically elongated, rounded to polygonal, parenchyma cells, measuring 20–110 μ in diameter and 40–300 μ in length; the wall between two adjacent cells is 1–6 μ thick. The parenchyma cells have sometimes partially decayed and separated before preservation.

EXPLANATION OF PLATE 1

Figs. 1, 2. *Palaeosmunda williamsii* gen. et. sp. nov. 1, Transverse section of holotype, UQF21571, from Corrievahn, $\times 2$; section from midway along specimen (top of Plate 2, fig. 1); transmitted and reflected light. 2, Details of stele, inner cortex, and part of outer cortex of fig. 1, $\times 8$; most of pith and inner cortex not preserved; leaf traces depart from stele with 2 protoxylem groups; transmitted light.

EXPLANATION OF PLATE 2

Figs. 1–7. *Palaeosmunda williamsii* gen. et. sp. nov. 1, 2, 6, 7, Holotype, UQF21571. 1, Longitudinal section, $\times 1$; lower half of specimen, details of pith not preserved. 2, Transverse section of petioles showing stipules, $\times 5$. 6, Transverse section from upper part of specimen, $\times 2$. 7, Central portion of fig. 6, $\times 6$; pith partly displaced; note endodermis of stem continuous with sclerotic cortex of root trace at right centre. 3–5, UQF53542, from Homevale. 3, Transverse section, $\times 2$. 4, Detail of stele, $\times 8$; leaf traces leave stele with 2 protoxylem groups. 5, Longitudinal section of pith and xylem of stem, $\times 16$. (1, 3, 6, 7, transmitted and reflected light; 2, 4, 5, transmitted light.)



1

2

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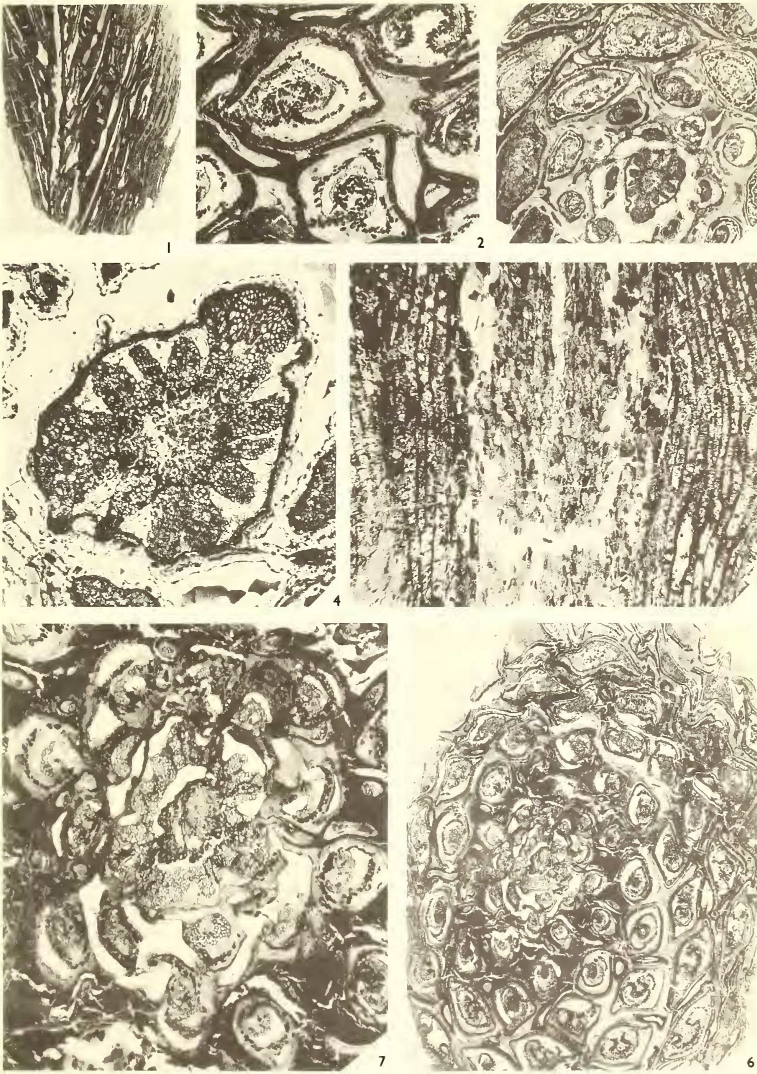

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In one specimen, a few short tracheids are present in the pith (Pl. 4, figs. 1, 2), but these occur where the stem is twisted and are associated with nearby metaxylem strands (cf. Hewitson 1962, p. 81). No internal endodermis is present.

The xylem cylinder is generally similar to that in *Osmunda* and *Osmundacaulis*. It is 0·7–2·2 mm. wide and in transverse section exhibits 0–9 gaps; i.e. in some specimens the xylem is a continuous, but indented ring (Pl. 1, fig. 2; text-fig. 3C, D), while in others it is dissected (Pl. 2, fig. 4; text-fig. 3A, B) and similar to those in most post-Palaeozoic forms of the Osmundaceae. In transverse section the xylem cylinder has 9–24 external lobes, while the cylinder itself consists of 15–28 radial strands, each 9–17 tracheids thick. The protoxylem tracheids, initially mesarch in metaxylem strands below departing leaf traces, are 6–40 μ in diameter, with a wall thickness of 3–14 μ between adjacent cells, and exhibit one series of scalariform pits on each longitudinal wall. Metaxylem tracheids are 35–260 μ in diameter (commonly 50–150 μ), with a wall thickness of 6–23 μ between two adjacent cells. The metaxylem tracheids show regular scalariform pitting in 1–5 vertical series on each wall (Pl. 3, fig. 8); the transverse bars of thickening are 1·1–4 μ thick and 1·5–7 μ apart.

In most of the specimens, except for a dark line marking the position of the endodermis, and strands of sclerenchyma, little cellular detail is preserved between the xylem cylinder and the outer cortex of the stem (Pl. 1, fig. 2; Pl. 2, figs. 3, 4; Pl. 3, fig. 2). A parenchyma xylem sheath, 1–3 cells thick, may be present. Phloem is only preserved in one specimen; it probably formed a continuous layer around the xylem. Metaphloem cells in the wedges between the xylem lobes have a diameter of 27–100 μ with a wall thickness of 3–6 μ. Outside the phloem is a layer of flattened cells up to 7 cells thick, which probably represents the protophloem and pericycle. The endodermis is marked by a dark line or a stained zone, and an abrupt change from pericycle tissue to inner cortex, but cellular detail is lacking. The endodermal diameter is 3·5–8 mm.

Cortex. The inner cortex is 0·8–5·5 mm. wide and consists of parenchyma with, in some specimens, bundles of sclerenchyma fibres. The parenchyma is polygonal to rounded in transverse section, and may be tangentially elongated, measuring 25–70 μ $\times$ 10–60 μ; thickness of the wall between two adjacent cells is 0·7–4 μ, but may appear up to 14 μ thick with deposits of organic and mineral matter. Where present, the bundles of sclerenchyma fibres occur in an intermittent peripheral zone around the endodermis below and adjacent to abaxial surfaces of the departing leaf traces (Pl. 1, fig. 2; Pl. 2, fig. 7); the bundles usually surround the endodermis of the leaf trace as it leaves the stele and they accompany it through the inner and outer cortex of the stem and into the petiole bases. In other cases however, the sclerenchyma does not appear until further out in the inner or outer cortex. In transverse section the bundles measure up to 540 μ tangentially, and up to 210 μ radially. They are composed of sclerenchyma fibres which have a diameter of 13–38 μ, a length of at least 850 μ, and a wall thickness between adjacent cells of 6–18 μ. The primary and secondary walls are clearly shown and the secondary wall may almost completely fill the cell. The inner cortex contains 5–24 leaf traces in a given transverse section.

The dense outer cortex is 2·5–9 mm. wide and consists of sclerenchyma fibres which are polygonal in cross section (Pl. 4, figs. 6, 7). The majority of these fibres have a diameter of 12–45 μ, sometimes up to 70 μ, and length of 270 μ to at least 1100 μ; the end walls are transverse, oblique, or tapering. The primary and secondary walls are clearly preserved and the secondary wall may consist of several layers. Total thickness of wall between two adjacent fibres is 6–30 μ; intercellular spaces of up to 4 μ are sometimes present at the angles. The longitudinal walls may be smooth or exhibit simple, small (3–7 μ), round to oval, irregularly scattered pits. Large, irregularly defined rectangular ($3\times 7\ \mu$–$7\times 23\ \mu$, 1·5–8 μ apart) or annular pits may also be present, but these appear to be formed by shrinkage of the original cell wall. Rare transverse septations may occur. Sometimes the lumen of a fibre is almost filled with secondary wall. A few layers of relatively larger and shorter, although otherwise similar, fibres occur adjacent to the inner cortex of the stem and leaf traces (Pl. 1, fig. 2), and also on the outside of the stem in the depressions behind the departing petioles (Pl. 4, fig. 8); these cells usually have a diameter of 40–85 μ, and a length of 70–300 μ. Part of the outer cortex of one specimen appears inhomogeneous with rings of light-coloured (in thin section) fibres surrounding the leaf traces, and darker, somewhat larger fibres in the areas between the rings (Pl. 3, fig. 1). The outer cortex contains 7–26 leaf traces in a given transverse section. Total number of leaf traces in any one transverse section of the whole cortex is 12–43.

Leaf traces. Traces are formed from the metaxylem strands of the stem in a manner generally similar to that in the subgenera *Osmunda* and *Osmundastrum* of the genus *Osmunda* (Hewitson 1962, Miller 1967). A protoxylem group develops approximately in the centre of the metaxylem strand which gives rise to the leaf trace. Above this point an island of parenchyma develops adaxially to the protoxylem group. This island enlarges upwards and usually becomes connected by a narrow gap with the pith. Thus the xylem strand assumes a U-shape with the narrow open end of the 'U' directed

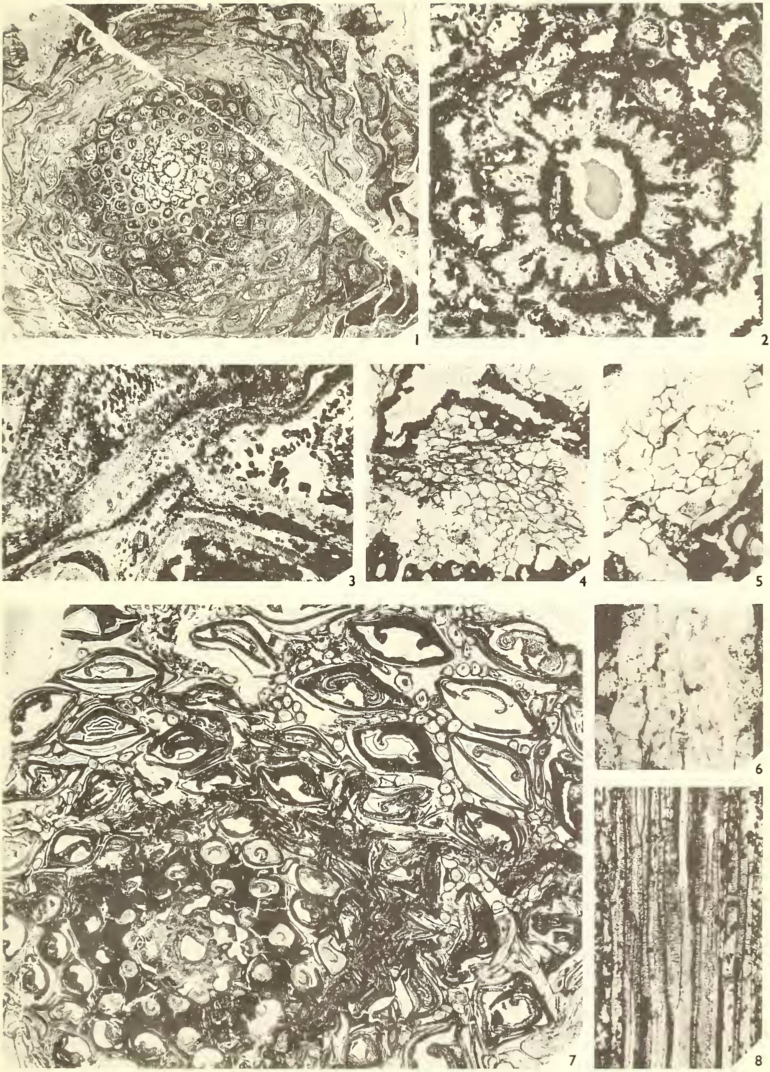
EXPLANATION OF PLATE 3

Figs. 1–8. *Palaeosmunda williamsii* gen. et sp. nov. 1–3, UQF57604, from Byerwen. 1, Transverse section, ×1. 2, Transverse section of stele; most of pith and inner cortex filled with silica; leaf traces arise with 1 protoxylem group, ×6. 3, Transverse section of parts of petiole bases showing irregular mass of sclerenchyma in sclerotic ring, and sclerenchyma strands in stipules, ×10·6. 4–6, UQF50624, from Blackwater district. 4, 5, Transverse sections of pith. 4, ×42; 5, ×67·5. 6, Longitudinal section of pith, ×67·5. 7, 8, UQF50620, from Blackwater district. 7, Transverse section, ×1·5; numerous roots and petioles loosely adpressed in outer part of mantle. 8, Longitudinal view of xylem tracheids of stem, ×42. (1, transmitted and reflected light; 2–8, transmitted light).

EXPLANATION OF PLATE 4

Figs. 1–10. *Palaeosmunda williamsii* gen. et. sp. nov. 1, 2, Longitudinal sections showing tracheids in pith, UQF50620. 1, ×42; 2, ×66. 3, Transverse section of roots, UQF53549, from Blackwater Mine, ×10·6. 4, 5, Longitudinal sections of xylem of root. 4, UQF50624, ×99; 5, UQF57604, ×63. 6, 7, Transverse sections of sclerenchyma fibres of outer cortex. 6, UQF53552, from Blackwater Mine, ×60, showing intercellular spaces; 7, UQF53549, ×60. 8, Longitudinal section of outer cortex and part of sclerotic ring of departing petiole, showing shorter fibres at outside of stem; longitudinal axis of section tilted to left; UQF53552, ×40. 9, Longitudinal section of sclerenchyma strand in inner cortex of petiole, showing pitting, UQF50624, ×99. 10, Transverse section of part of petiole base, UQF53541, from Homevale, ×42; note increase in diameter of fibres of sclerotic ring towards inner cortext of petiole.

Fig. 11. *Palaeosmunda playfordii* gen. et. sp. nov. Transverse surface of holotype, UQF53544, from Blackwater Mine, ×0·75; loosely adpressed petioles and numerous roots in outer part of mantle. (1–10, transmitted light; 11, reflected light.)



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